

# PSYCHE

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Vol. 82

March, 1975

No. 1

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## MEGASECOPTERA FROM THE LOWER PERMIAN OF MORAVIA\*

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The Megasecoptera are separated from the closely related Paleozoic Order Palaeodictyoptera by having nearly homonomous, elongate, petiolate (or basally narrowed) wings; usually a simple venation; and Sc and R crowded towards the costal margin. The body structures in both orders are virtually identical, so far as known. The relationship of these groups gives the impression of being like that between dragonflies and damselflies within the Order Odonata, rather than that between two different orders (Kukalova-Peck, 1973). Only recently has the wing attachment to the body in both groups been studied (Kukalova-Peck, 1974), revealing evidence which justifies the recognition of Megasecoptera as a distinct order. The Palaeodictyoptera have been found to retain many features of the primitive paleopterous wing base, such as the fully developed subcostoanal axillary plate. In the Megasecoptera, however, the subcostoanal axillary plate is missing and the axillary sclerites are highly specialized and largely fused. The morphology of the axillary region in Megasecoptera is unique within the Paleoptera and shows once again the potential for extraordinary diversity in the paleopterous orders.

The Lower Permian locality of Obora in Moravia (Czechoslovakia) has recently yielded twelve specimens of Megasecoptera, referred here to six new families: Caulopteridae, Hanidae, Arcioneuri-

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\*This study has been supported in part by grant no. GB 39790 from the National Science Foundation (F. M. Carpenter, Principal Investigator, Harvard University) and in part by a publication grant of Carleton University, Ottawa, Canada. I am deeply indebted to Dr. Frank M. Carpenter for critical review of the manuscript and for his manifold support of my work.

*Manuscript received by the editor April 26, 1975*

dae, Ancopteridae, Engisopteridae and Alectoneuridae, in addition to the families Bardohymenidae and Moravohymenidae, already reported in a previous paper (Kukalova-Peck, 1972). One of the new species, *Hana lineata*, with a wing about 100 mm long and only 8.3 mm wide, represents an extreme case of specialization of wing shape within the Insecta. Further evidence of the close relationship in wing venation between Megasecoptera and Palaeodictyoptera is now revealed. The postcostal vein, homologous with the "costal brace" in the Ephemeroptera and present in most Palaeodictyoptera, is recognizable in the family Engisopteridae. Intercalated sectors, which also occur in several families of the Palaeodictyoptera, as well as in all dragonflies and mayflies, are present in five of the new genera described below. Also, some of the new species have relatively broad subcostal areas and a richly branched venation very reminiscent of the Palaeodictyoptera.

The Upper Carboniferous (Westphalian) families Frankenholziidae (Germany), Mecynopteridae (Belgium) and the new family Dictyoneurellidae (France) (described below), all of which were previously considered palaeodictyopterous, are apparently related to the newly described families mentioned above and to the primitive family Anchineuridae (Upper Carboniferous, Spain) of the Order Megasecoptera. They are herein referred to that order.

Besides the adults, three nymphal forms are described: *Cauloptera colorata*, *Arcioneura juveniles*, and *Alectoneura europaea*. The nymphal wings are easily distinguished from the adult wings, which are held at right angles to the body, by the characteristic bend in the proximal third of the wing length. This bend determined the oblique-lateral position of the wing pads in the living nymphs, as described by Carpenter and Richardson (1968) in the completely preserved early stage of the megasecopteran nymph of *Mischoptera douglassi*. However, in all isolated nymphs from Obora the angle of the bend is more obtuse than in *Mischoptera douglassi*. This fact together with the larger size and good sclerotization of the venation (the sclerotization being weak in *douglassi*) implies that the nymphal wings from Obora belonged to late, possibly the ultimate, instars. There is no evidence as to whether or not a subimaginal stage was present in Megasecoptera. In the Palaeodictyoptera, parts of a shed cuticle have been found attached to a female of *Lycocercus goldenbergi* (Kukalova, 1969, p. 449, fig. 32), including a smaller and less sclerotized ovipositor than that of the adult. It is therefore conceivable that the related Megasecoptera, which clearly descended from the Palaeodictyoptera, had adult molts.

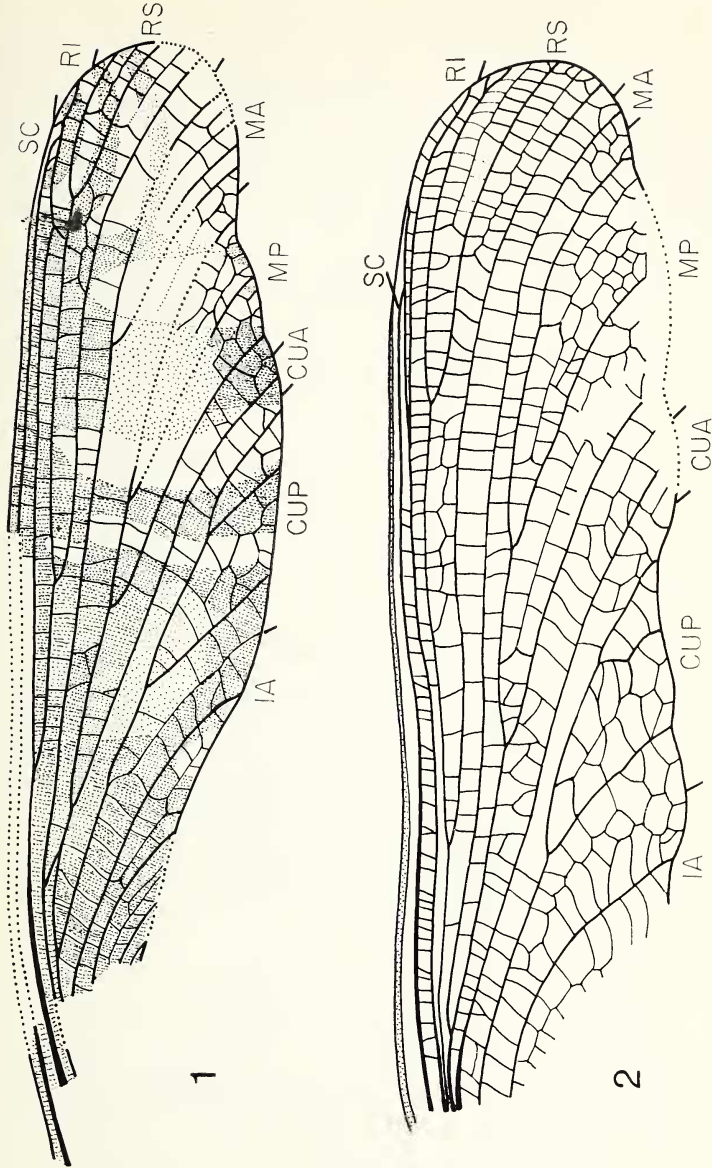


Fig. 1. *Cauloptera colorata* n.sp., specimen 24/1974. Wing fragment, length 38 mm, width 9 mm. Holotype.  
Fig. 2. *Ancoptera permiana* n.sp., specimen 30/1974. Wing fragment, length 36 mm, width 9.8 mm. Holotype.

### Family **Caulopteridae**, new Family

Nymphal wing: petiolate, broadened beyond mid-wing, narrowed in the apical third; posterior margin undulated. Sc long; stems of R and M not coalesced in the basal third; Rs diverging from R1 before mid-wing; MA and MP branched; MP anastomosed with CuA for a short distance; CuA simple, CuP sending off several branches; 1A with a series of branches. Cross veins numerous, irregular, forming intercalated sectors.

This family differs from the Anchineuridae in the petiolation of the wing, the branched MA and the coalesced MP and CuA.

Although the shape of the wing in the family Caulopteridae and in the following three families is specialized and typical for Megasecoptera, the venation is reminiscent of that in the Palaeodictyoptera. If the proximal, narrow part of the wing has not been preserved, the megasecopterous character of such a fragment would be obscure. This seems to be true for several incompletely preserved wings previously considered palaeodictyopterous, discussed below.

At present this family includes only the following genus:

### **Cauloptera**, new genus

Nymphal wing: moderately slender, with a broad lobe in the third quarter of the wing length; posterior margin undulated beyond mid-wing only within the mp area. Sc, R1 and Rs equally distant from each other, close to, but not crowded towards the costal margin; Rs with 2 long branches; MA with several short branches.

The generic name is derived from the Greek words *kaulos* and *ptera* (petiole + wings) and is considered neuter plural.

Type species: *Cauloptera colorata*, n.sp.

### **Cauloptera colorata**, n.sp.

#### Figure 1

This species is based on a detached, well-preserved wing pad of a late nymph; the base is narrowed, perhaps petiolate; the basal third is missing.

Nymphal wing: length (estimated) about 41 mm, width 9 mm. Broadened part of the wing forming a smooth, broad lobe; undulations in the mp area shallow; apex comparatively broad and rounded.



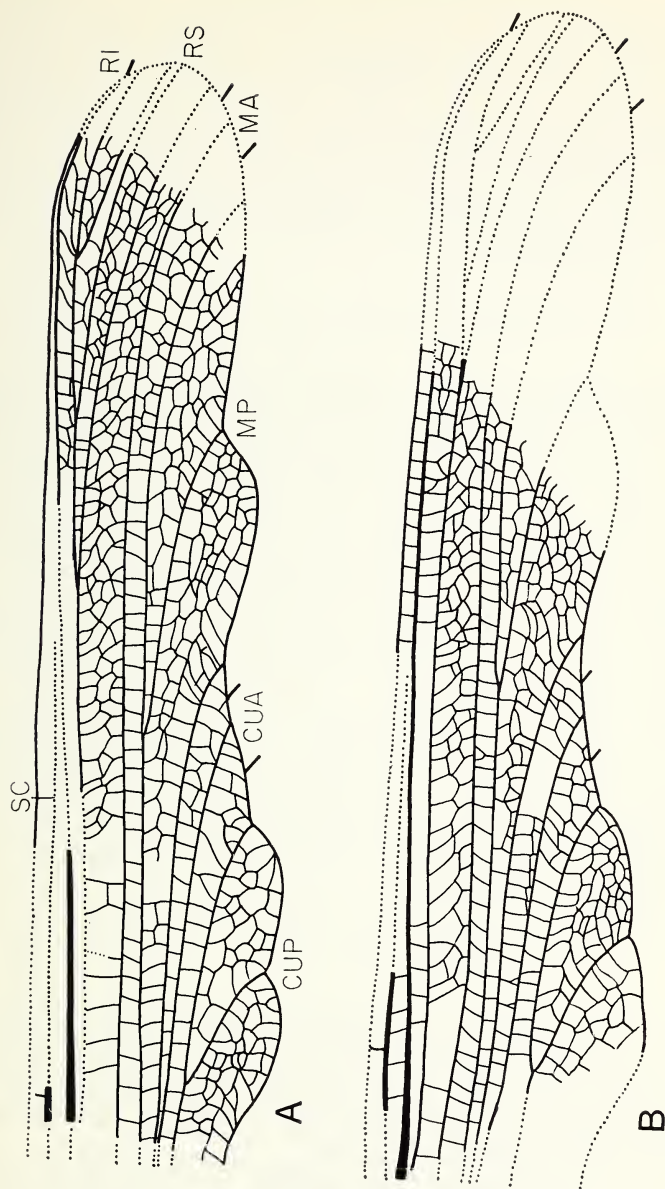


Fig. 3. *Hana flia* n.sp., specimen 25/1974. A. Fore wing fragment, length 45 mm, width 9 mm; B. Hind wing fragment, length 38 mm, width 11 mm. Holotype.

Sc terminating on R1; Rs originating before mid-wing; MA sending off 3 branches; MP with 2 branches; CuA simple, CuP with 2 branches; 1A with a series of about three branches; intercalated sectors mostly short. Wings dark-colored, with irregular light bands becoming crescent in the apical area.

Holotype: No. 24/1974; wing fragment, length 38 mm, width 9 mm; obverse. Paleontological Institute of Charles University, Prague, Czechoslovakia.

### Family **Hanidae**, new family

Wing: petiolate, broadened at about mid-wing, narrowed in cua area; posterior margin deeply undulated. Venation simplified; Sc terminating shortly beyond mid-wing; stems of R and M not coalesced in the basal third; Rs diverging from R1 about mid-wing; MA and CuA simple, MP and CuP with few branches; MP anastomosed with CuA for a short distance; 1A simple. Archedictyon and irregular cross veins present. Intercalated sectors absent.

The family Hanidae differs from the related family Caulopteridae in the more deeply undulated posterior margin, in the short Sc, the simplified venation, the presence of the archedictyon and in the absence of the intercalated sectors.

The large, elongate, extremely narrow wings of Hanidae, with an intricate outline, are among the most unusual wings within the Paleoptera. The preservation of a primitive archedictyon, which in other families becomes reduced to cross veins by Westphalian time, is a remarkable example of mosaic evolution in Paleozoic Paleoptera.

Type genus: *Hana*, new genus.

### **Hana**, new genus

Wing: very long and narrow; posterior margin forming several prominent lobes in the median and cubital areas. Sc distant from anterior margin in the basal half of the wing; Rs with about 3 short branches; 1A following closely the posterior margin. Wing membrane with a dense covering of tubercles.

This genus is represented by two species: *H. filia*, based on the distal half of a wing, and *H. lineata*, n.sp., based on the proximal half of a wing. The genus is named for my daughter Hana, who has been very helpful to me in the field work.

***Hana filia*, n.sp.**

Figures 3-6a

This species is based upon beautifully preserved distal halves of the fore and hind wings, in normal positions (see reconstruction of the outlines, fig. 6a). The hind wing is somewhat longer and broader at the end of the anal area than the fore wing. The venation is almost identical in the wings, though the first branch of Rs originates more markedly distally in the hind wing. In both wings, the costal margin is proximally broken away; in the fore wing, the posterior part of the wing is superimposed over R. Both wings are restored to the original widths in figure 3.

Besides the holotype, a small fore wing fragment (specimen no. 26/1974, fig. 4), and a hind wing fragment (specimen no 27/1974, fig. 5) were found, showing a coloration and a lobation of the posterior margin remarkably similar to that of the holotype.

Wings: length of the fore wings about 84 mm, width 10.5 mm; length of the hind wing about 88 mm, width 12 mm. Posterior margin deeply incised at the end of all branches of CuP and at MP<sub>2</sub>; Rs originating before mid-wing, Rs branches originating in the distal quarter of the wing; MA and CuA simple; MP with 2 branches, CuP probably with 1 short branch; archedictyon and cross veins strong, conspicuous. Wing membrane covered with numerous prominent tubercles and with extensive, irregularly outlined dark areas; hind wings darker than fore wings.

Holotype: no. 25/1974 (fore wing fragment, length 45 mm, width 9 mm; hind wing fragment, length 38 mm, width 11 mm; obverse and reverse); specimen no. 26/1974 (fore wing fragment, length 33 mm, width 9.5 mm; obverse and reverse); specimen no. 27/1974 (hind wing fragment, length 19 mm, width 8.4 mm; obverse and reverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

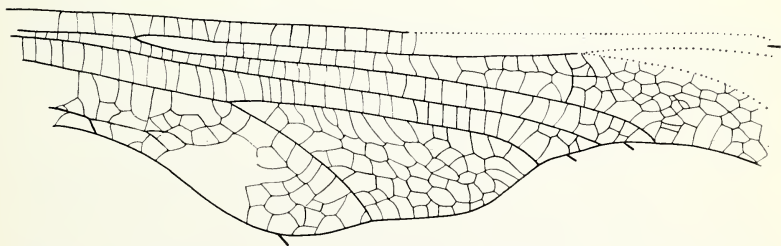


Fig. 4. *Hana filia* n.sp., specimen 26/1974. Fore wing fragment, length 33 mm, width 9.5 mm.

**Hana lineata**, n.sp.

Figures 6b and 7

This species is based upon the proximal half of the longest and narrowest wing known in the Megasecoptera (see reconstruction, fig. 6b). The subcostal area is proximally partially superimposed across R. In figure 7 the venation is shown restored to its normal position.

Wing: length about 96 mm, width 8.3 mm. Posterior margin convexly bent at the end of all branches of CuP; Rs originating beyond mid-wing; first branch of MP long, starting before mid-wing; CuP with a series of 3 short branches; archidictyon and cross veins similar to those of *filia*, but finer. Wing membrane densely covered with small tubercles. A few dark spots occur in the subcostal area.

This species differs from *filia* in its narrower wings, finer membrane and its series of 3 CuP branches.

Holotype: no. 28/1974 (wing fragment, length 58 mm, width 8.3 mm; reverse). Paleontological Institute of Charles University, Prague.

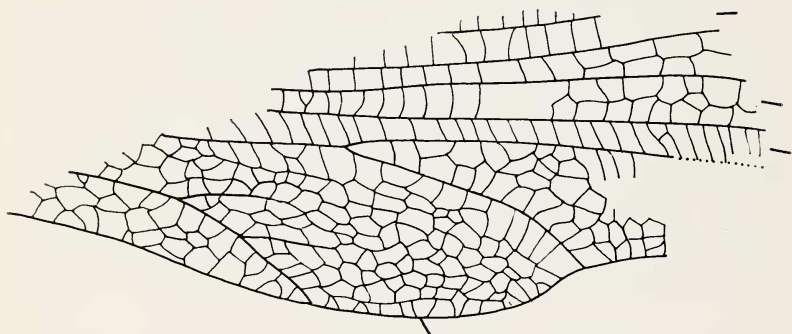


Fig. 5. *Hana filia* n.sp., specimen 27/1974. Hind wing fragment, length 19 mm, width 8.4 mm.

**Family Arcioneuridae**, new family

Nymphal wing: petiolate, narrow, broadened at about mid-wing; posterior margin undulated. No coalescing veins; Sc short; Rs diverging from R1 well before mid-wing; MA and MP with several branches; CuA and CuP with few short branches. Cross veins numerous, forming intercalated sectors.

This family differs from the Caulopteridae in the shorter Sc and in lacking the coalesced MP and CuA. Type genus: *Arcioneura*, new genus.

### *Arcioneura*, new genus

Nymphal wings: very long and narrow. R1 close to the costal margin in the distal half of the wing; Rs with about 2 long branches; MA with a series of short branches; MP forming a long branched fork. Cross veins almost regular.

The generic name is derived from the Greek words *arkios* and *neura* (certain + veins) and is considered neuter plural.

Type species: *Arcioneura juveniles*, n.sp.



Fig. 6. Hanidae, reconstruction of the specialized wing outline. A. *Hana filia* n.sp., fore and hind wing in natural position. Fore wing, length about 84 mm, width 10.5 mm. B. *Hana lineata* n.sp. Wing, length about 96 mm, width 8.3 mm.

### *Arcioneura juveniles*, n.sp.

#### Figure 8

This species is based upon a detached wing of a nymph, bent typically into oblique-lateral position in the basal third. The slight angle of the bend and the advanced sclerotization of veins and cross veins indicate that the nymph was close to the adult stage.

Nymphal wing: length about 19 mm, width 2.6 mm. Sc terminating shortly beyond mid-wing; Sc much closer to R and R1 than to the costal margin; Rs detaching from R1 at the end of the basal third, the first branch of Rs starting shortly beyond mid-wing; MA sending off 4 branches, MP probably 3 times branched; CuP with 1 branch; 1A probably simple.

Holotype: no. 29/1974 (almost complete wing, length 18.3 mm, width 2.6 mm; reverse). Paleontological Institute of Charles University, Prague.



**Anconeura**, new genus

Wings: very long and narrow; posterior margin undulated beyond mid-wing. R1 close to the costal margin; Rs with about 4 long branches, sometimes forked; MA with a series of short branches; MP with a long, branched fork; CuA forked. Cross veins irregular.

*Anconeura* differs from *Arcioneura* by its larger wings, which have more numerous branches on Rs and CuA. The generic name is derived from the Greek words *ankos* and *neura* (curve + veins) and is considered neuter plural.

Type species: *Anconeura havlatai*, n.sp.

**Anconeura havlatai**, n.sp.

## Figure 9

This species is monotypic, based upon an adult wing with a well preserved, long, petiolate base. Distally from mid-wing, the wing is broken into several dislocated pieces. In figure 8, the venation is shown restored to its normal pattern.

Wing: length about 41 mm, width 5.7 mm. Wing broadest shortly beyond mid-wing; posterior margin with 4 undulations; at its proximal end the petiole broadens for its attachment to the thorax. Rs originating at about the end of the basal third, the first branch of Rs starting before mid-wing; MA sending off 3 branches; MP probably branched 4 times; CuA probably branched 5 times; CuP with 1 branch. 1A close and parallel with the posterior margin, with one branch.

Holotype: no. 23/1974 (almost complete wing, length 40 mm, width 5.7 mm; obverse). Paleontological Institute of Charles University, Prague.

The species is named for Karel Havlata of Prague, who has collected hundreds of specimens of insects in the Obora beds.

Family **Ancopteridae**, new family

Wings: elongate; almost equally broad beyond mid-wing; posterior margin undulated. Sc somewhat shortened; stems of R and M not coalesced in the basal third; Rs diverging from R1 much before mid-wing; MA and CuA simple, MP and CuP branched. Cross veins numerous, forming conspicuous intercalated sectors.

The family Ancopteridae differs from the related family Dictyoneurellidae (Westphalian, France), and Anchineuridae (U. Carboniferous, Spain) in the presence of the undulated posterior margin,

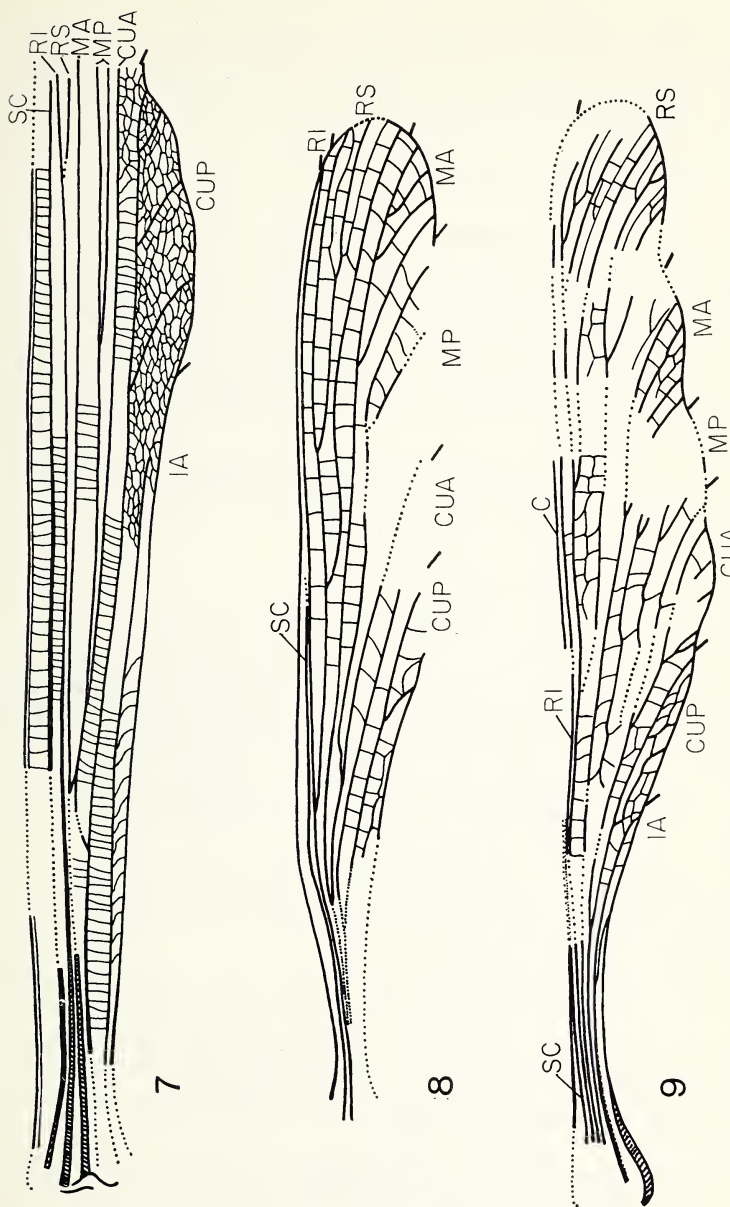


Fig. 7. *Hana lineata* n.sp., specimen 28/1974. Wing fragment, length 58 mm, width 8.3 mm. Holotype.  
 Fig. 8. *Arcioneura juvenales* n.sp., specimen 29/1974. Wing, length 18.3 mm, width 2.6 mm. Holotype.  
 Fig. 9. *Anconeura havelatai* n.sp., specimen 23/1974. Wing, length 40 mm, width 5.7 mm. Holotype.

in the longer Rs and in the branching of the main veins, which generally arise much more basally. From the Arcioneuridae it differs in the longer Sc, in the simple MA and CuA; from the Caulopteriidae in the simple MA and the absence of coalescence between MP and CuA.

Type genus: *Ancoptera*, new genus.

### **Ancoptera**, new genus

Wings: long but only slightly narrow, with broadly rounded apex; posterior margins with only shallow undulations. C broad, flattened; Sc and R1 crowded towards the costal margin in the distal third, but well remote from it proximally; Rs with 2 long branches; stem of R, stem of M and CuA touching each other in the proximal third of the wing; mp area large.

The generic name is derived from the Greek words *ankos* and *ptera* (curve + wings) and is considered neuter plural.

Type species: *Ancoptera permiana*, n.sp.

### **Ancoptera permiana**, n.sp.

#### Figure 2

This species is based upon a well preserved adult wing, with the narrowed basal part missing. The long anterior branch of R1 is probably only an individual variation. Besides the holotype, another specimen (no. 31/1974, fig. 10) was found, this being the distal part of a wing. In this wing fragment, the apical part is more pointed and the Rs branches are much shorter than in the holotype. The veins and cross veins are surrounded by dark-colored, narrow bands, as in *Dictyoneurella*. Specimen no. 31/1974 probably belongs to a separate species, but because of the small size of the fragment it is referred here to *Ancoptera* sp.

Wing: length about 43 mm, width, 9.8 mm. Posterior margin with 4 undulations in the distal part of the wing, Rs diverging from R1 at about the first fifth of the wing length; first branch of Rs originating much before mid-wing; MP with a series of 3 branches; CuP forming a wide fork, mp-cua area and cup-anal area are wide. Intercalated sectors long and regular.

Holotype: no. 30/1974 (wing fragment, length 36 mm, width 9.8 mm; obverse and reverse); specimen no. 31/1974 (wing fragment, length 31.5 mm, width 10.7 mm; reverse). Paleontological Institute of Charles University, Prague.

Family **Engisopteridae**, new family

Wings: narrow, but not petiolate, almost uniformly broad in distal half; posterior margin not undulated. Postcostal vein present; Sc terminating shortly before mid-wing, subcostal area relatively broad; Rs short; ma area large and rich in long branches, mp area narrow; CuA simple, CuP with long branches. Cross veins numerous, intercalated sectors present.

This family differs from the Arcioneuridae in the broader wings, the presence of the postcostal vein, the shorter Rs, and larger ma and cup areas. From the primitive family Archineuridae it differs in its relatively broad subcostal area, short Sc and Rs and in the more nearly parallel arrangement of median and cubital branches.

The family Engisopteridae has several characteristics of venation which are among the most primitive known in the Megasecoptera: the relatively broad subcostal area with a series of Sc branches, the postcostal vein, and the generalized, richly branched venation (except for a simple CuA). These particular features are palaeodictyopterous in character, and they are more primitive than their structure in Archineuridae.

The postcostal vein, which I consider homologous with the "costal brace" of Ephemeroptera, is present in almost all Palaeodictyoptera. In addition to the Engisopteridae, the vein has been found in the Mischopteridae (Carpenter & Richardson 1968, fig. 1, 2), in both adult and nymphal wings. It is probable that this inconspicuous vein has been overlooked in several other families. The postcostal veins are completely reduced in families with a convexly bent Sc at the very base, as in Protohymenidae or Alectoneuridae.

**Engisoptera**, new genus

Wings: more or less elongate-oval in shape, narrowed across the anal area. C, Sc and R1 equidistant from each other in the distal half of the wing; Sc terminating on C; Rs very remote from R1, sending off 2 short branches; MA, MP, and CuP branches originating very anteriorly. Cross veins almost regular.

The most conspicuous character of this new genus is the branches of the main veins originating very anteriorly in the wing. A similar branching pattern is present in the hind wings of some Palaeodictyoptera.

The generic name is derived from the Greek words *engys* and *ptera* (near + wings) and is considered neuter plural.

Type species: *Engisoptera simplices*, n.sp.

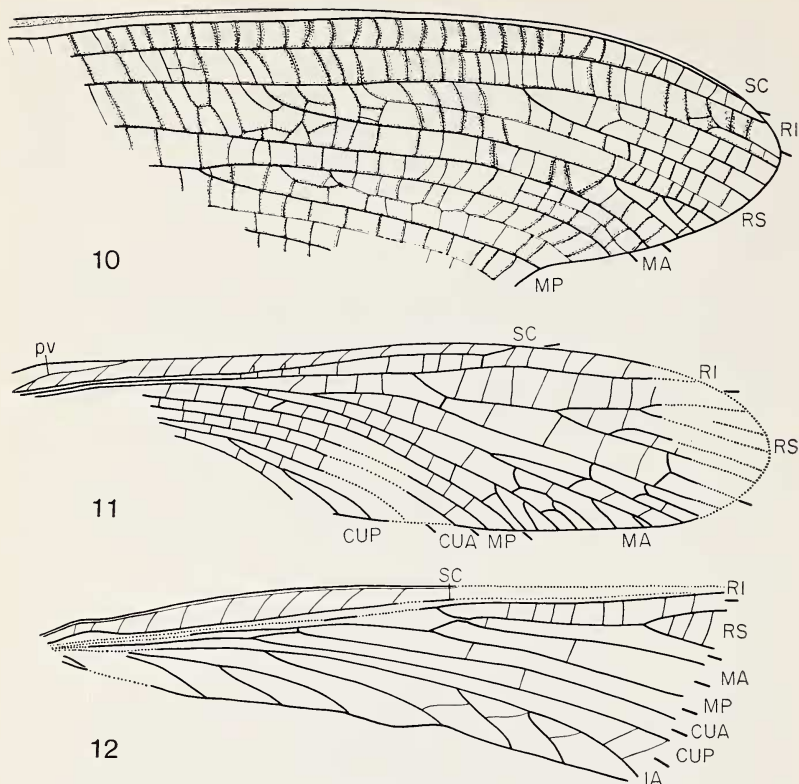


Fig. 10. *Ancoptera* sp., specimen 31/1974. Wing fragment, length 31.5 mm, width 10.7 mm. Original.

Fig. 11. *Engisoptera simplices* n.sp., specimen 32/1974. Wing fragment, length 18 mm, width 4 mm. Holotype. pv = postcostal vein.

Fig. 12. *Alectoneura europaea* n.sp., specimen 33/1974. Wing fragment, length 12.8 mm, width 3.3 mm. Holotype.

### *Engisoptera simplices*, n.sp.

#### Figure 11

This species is based upon a detached, very delicate wing with the anal area and the apical area missing.

Wing: length about 20 mm, width 4 mm. Rs diverging from R1 shortly beyond mid-wing, rs area small, triangular; MA with 2 long branches, the distal one twice branched; MP with a single, long parallel branch; CuP with a series of several relatively long branches. Intercalated sectors almost regular, well-pronounced.



Holotype: no. 32/1974 (wing fragment, length 18 mm, width 4 mm; obverse). Paleontological Institute of Charles University, Prague.

Family **Alectoneuridae**, new family

Wings: very narrow in the proximal third but not petiolate, broadest beyond mid-wing. Venation simplified; Sc terminating before the apical third; stems of R and M not coalesced in the basal third; Rs diverging from R1 before mid-wing; MA adjoining or coalescing with Rs for a short distance. 1A with a series of long branches. Cross veins few.

The venation of Alectoneuridae is very close to that of Mischopteridae. However, the shape of the wing is less specialized in lacking the petiole, and the anal area has a more generalized venation. The basal part of the wing, including the convex basal bend of the subcosta, is very reminiscent of the Protohymenidae (Kukalova-Peck, 1974).

The Alectoneuridae combines morphological features of two groups of families, which originated from common ancestors: Mischopteridae, Sphecopteridae, Carbonopteridae, Ischnoptilidae, Corydaloididae, Foririidae on one side; and Aspidothoracidae, Scytomyzidae, Aspidohymenidae, Vorkutiidae, Bardohymenidae, and Protohymenidae on the other side. The family Alectoneuridae probably descended from the ancestors of both groups and has a morphologically intermediate position similar to that of the Moravohymenidae (Kukalova-Peck 1972, p. 256).

Type genus: *Alectoneura*, new genus.

**Alectoneura**, new genus

Wing: C and Sc convexly bent before the base; subcostal area relatively broad in the proximal half of the wing, with a series of Sc branches; M dividing into MA and MP at the level of the origin of Rs; anal area relatively broad and long, reaching beyond mid-wing.

In its venation, *Alectoneura* recalls *Psilothorax* (Mischopteridae); and in the structure of the basal part of the wing, *Protohymen* (Protohymenidae). The broad subcostal area, with a series of numerous subcostal branches and the relatively large anal area with richly branched 1A, are the characters typical for primitive Megaseoptera with generalized venation.

The generic name is derived from the Greek words *alecto* and *neura* (indescribable + veins) and is considered neuter plural.

Type species: *Alectoneura europaea*, n.sp.

**Alectoneura europaea**, n.sp.

## Figure 12

This species is based upon a single wing, which is slightly bent at the end of its basal quarter. The wing might have belonged to a subimago of a species like *Sphecoptera elegantissima*, since all other wings in all related families are straight in the basal part. In this case, the deep concavity of the posterior margin at the 3rd branch of 1A would probably become less pronounced in the adult wing. In the holotype, the very fine wing membrane has split along the veins and become slightly superimposed posteriorly over other parts of the membrane. In figure 12, the venation is restored back into normal position.

Wing: length of the fragment 12.8 mm, width 3.3 mm. Anterior margin broadly bent in the basal quarter; posterior margin slightly undulated at about the middle of the anal area; Sc close to R along its whole course; Rs and MA adjoining for a short distance; first branching of Rs broadly dichotomous; M and Cu branches almost parallel and probably simple; CuA soon after its origin connected with M by a short cross vein; 1A with 4 long branches; 2A short, simple. Cross veins near the posterior margin sigmoidal, almost parallel with the longitudinal axis.

Holotype: no. 33/1974 (obverse and reverse). Paleontological Institute of Charles University, Prague.

## THE PROBLEM OF RECOGNIZING GENERALIZED MEGASECOPTERA

Before this new material from Moravia was made known, megasecopteran wings were readily separated from those of the Palaeodictyoptera by the crowding of Sc and R towards the costal margin, the basally narrowed wings, and the simplified venation (Carpenter, 1963). However, with the presence of a rather broad subcostal area in Ancopteridae, Alectoneuridae, Engisopteridae and Hanidae, and the richly branched venation in Caulopteridae, Arcioneuridae and Engisopteridae, the recognition of primitive Megasecoptera becomes more difficult. This is true especially for fragmentary wings, in which the proximal, narrow part may not be preserved.

For identifying Megasecoptera with a generalized venation, the most reliable criteria are as follows: long, nearly homonomous wings; a narrow anal area; at least a partial crowding of Sc and R towards the costal margin; and the wing conspicuously broad at about mid-wing but narrowed both proximally and distally. An irregular and

not very dense cross venation, coarse archdictyon, and incomplete intercalated sectors are often present. However, each single feature mentioned above occurs randomly in the Palaeodictyoptera and should be carefully considered if found separately.

Keeping in mind the similar features of primitive megasecopterous and palaeodictyopterous venation, I believe that the following species, based upon fragments and previously considered to belong to the Palaeodictyoptera, need to be reconsidered for possible inclusion within the Megasecoptera.

*Dictyoneurella perfecta* Laurentiaux, 1949 (Westphalian, northern France) is probably megasecopterous because of the shape of the wing, which is broadest at the middle, and narrowed both proximally and distally; and because of the general resemblance to Anchineuridae and Anconopteridae. This species is herein referred to a new family, **Dictyoneurellidae**, characterized by having a simple lobe on the posterior wing margin, and a primitive venation that lacks coalescence of veins, a relatively broad subcostal area, simple MA and CuA, richly branched MP and CuP, and irregular cross veins forming intercalary sectors.

The family Frankenholziidae, based on *Frankenholzia culmani* Guthörl, 1962 (Lower Westphalian D, Germany) is in all probability megasecopterous, since the wing is broadest at mid-wing and narrows distally and proximally. It differs from the Arcineuridae by having broader wings, a broad lobe on the posterior margin and by less abundant cross veins [The vein marked by Guthörl, 1962, fig. 3, as Sc is in reality R1, R is Rs, and A is CuP].

The family Mecynopteridae, based on *Mecynoptera splendida* Handlirsch, 1904 (Westphalian C, Belgium), is almost certainly megasecopterous, because Sc and R1 are crowded towards the costal margin and the wing is elongate. It is related to the Upper Carboniferous Anchineuridae and Dictyoneurellidae and to the Lower Permian Ancopteridae, all characterized by the presence of irregular cross veins and intercalated sectors. *Mecynoptera tuberculata* Bolton, 1921, is a wing fragment too small to be referred to any particular genus; and *Merlenbachia grimaldi* Waterlot, 1934, classified by its author in the Mecynopteridae, is a wing fragment of dubious systematic position, and may even be neopterous.

*Saardictyum abnormis* Guthörl, 1939 (Westphalian D, Germany) is very probably megasecopterous, because of the typical narrowing of the wing towards the base, almost into a petiole. Very likely it represents a separate family with primitive venation and a dense archdictyon, and rather broad subcostal area. Unfortunately, the

venation of the holotype is misinterpreted in the original figure (Guthörl, 1939, fig. 1), and the type specimen, which was deposited in a private collection, is not accessible for study. Hence, this species is referred to the Megasecoptera, family uncertain.

*Orthocosta lithomantidoides* Waterlot, 1934 (Westphalian C, Belgium) is based upon a small wing fragment. Because of the shape of the posterior margin and the irregular cross venation, with incompletely developed intercalated sectors, I believe it belongs to the Megasecoptera, though of uncertain family position. *Orthocosta splendens* Bolton, 1912, on the other hand has a loose "palaeodictyopterous" type of reticulation and is referred here to the Palaeodictyoptera, uncertain family position.

*Palaeopalara gracilis* Handlirsch, 1904, and *Antracopalara falcipennis* Handlirsch, 1904 (Westphalian C, Belgium) are small wing fragments with megasecopterous wing shape. Both species are here referred to the Megasecoptera, families uncertain.

Since it seems clear that the most primitive Megasecoptera merge fully in the wing venation pattern with the Palaeodictyoptera, we must accept the fact that some little-known species cannot be identified to either order with certainty.

The following is a summary of my present concept of the relationships of the species mentioned above:

#### Order Megasecoptera

Family Dictyoneurellidae Kukalova-Peck (herein described)

*Dictyoneurella perfecta* Laurentiaux, 1949

Family Frankenholziidae

*Frankenholzia culmani* Guthörl, 1962

Family Mecynopteridae

*Mecynoptera splendida* Handlirsch, 1904

Family uncertain

*Saarodictyum abnormis* Guthörl, 1939

? genus *lithomantidoides* Waterlot, 1934

*Palaeopalara gracilis* Handlirsch, 1904

*Antracopalara falcipennis* Handlirsch, 1904

? genus *tuberculata* Bolton, 1921

#### Order Palaeodictyoptera

Family uncertain

*Orthocosta splendens* Bolton, 1912

#### Order uncertain

*Merlenbachia grimaldi* Waterlot, 1934

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